

The Effects of Forebrain Lesions on Mating Behavior in the Male Platyfish, *Xiphophorus maculatus*¹

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(Text-figure 1)

IN recent years numerous investigators have been concerned with the relation of the forebrain to sexual behavior in mammals (Beach, 1942, 1947), but comparable studies on lower vertebrates are limited. This is particularly true for teleosts. The live-bearing fishes are especially suited for a comparative study since reproductive behavior in these fishes consists of a series of patterns which are at least analogous to precopulatory and copulatory behavior in mammals. Among these fishes the poeciliid live-bearers such as the platyfish, swordtail and guppy are most useful, since their reproductive anatomy, physiology and behavior have been investigated to a greater extent than in any other teleost group.

Early investigators interested in forebrain function in fishes postulated that this region of the brain was primarily concerned with olfaction or with olfaction and its correlation with taste (Herrick, 1922). These concepts were based essentially on neuro-anatomical evidence from studies on the Chondrichthyes (cartilaginous fishes) and on certain of the more primitive Osteichthyes (bony fishes) where olfaction and taste play a predominant role in the sensory

repertoire. Although numerous scattered reports, pointing to a more generalized facilitative function of the forebrain of fishes not immediately related to olfaction, have appeared during the last few decades, the early concept of olfaction is still adhered to quite widely.

Experimental studies on forebrain lesions and extirpations in fishes have been reviewed by Ten Cate (1935). Various investigators reported no changes in locomotion, equilibrium, vision, feeding or conditioned responses to optic stimuli. Electrical stimulation of the intact forebrain produced no motor responses. Olfaction was abolished, as would be expected. However, Vulpian (1866), Janzen (1932), Hosch (1936) and Berwein (1941) have reported a general loss of responsiveness which they variously termed reduction in "arbitrary movements," "initiative," "irritability," and the like. Kumakura (1928), Noble (1936) and Wiebalck (1937) observed that schooling, which is primarily a visually directed response, was impeded in forebrainless fishes of several species.

The first studies in fishes that were oriented directly toward explaining the function of the forebrain in sexual behavior were those of Noble (1936, 1937, 1939a, 1939b), who reported, in a series of abstracts, that lesions in the corpus striatum (cerebral hemispheres or olfactory lobes in our terminology) in several species of cichlid and poeciliid fishes resulted in a loss of synchronization between the male and female in spawning and parental care. Noble & Borne (1941) reported that unilateral forebrain ablation caused no discernible alteration in sexual behavior in the oviparous *Betta splendens* and *Hemichromis bimaculatus*, although bilateral extirpation of the telencephalon caused complete cessation of sexual activity. However, in the

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viviparous poeciliid *Xiphophorus helleri*, complete removal of the forebrain had no effect on mating behavior. Aronson (1948), investigating the specific acts comprising spawning in the West African mouthbreeding cichlid *Tilapia macrocephala*, reported that early courtship patterns were only slightly affected by hemidecerebration or total decerebration. Those patterns more immediately related to spawning were markedly reduced in frequency of occurrence, especially by the more drastic lesions.

MATERIALS AND METHODS

The present study was performed on 27 sexually mature virgin male platyfish, *Xiphophorus (Platypoecilus) maculatus*. Throughout the experiment the fish were isolated in separate two-gallon aquaria, the rear and sides of which were painted an opaque blue to exclude external disturbances. The aquaria were situated in a greenhouse maintained at approximately 25° C.

Prior to operation, the males were deeply anesthetized in a 3 percent urethane solution and were then wrapped in a piece of cotton soaked in the anesthetic so that only the dorsal surface of the head was exposed. Under a dissecting microscope, an opening approximately 2 × 3 mm. was made in the roof of the skull between the eyes with a pair of iridectomy scissors, thus exposing the forebrain. Varying portions of the forebrain were then ablated with a low pressure aspirator. Bleeding was negligible. The fish were then placed in aquarium water to which 0.8% Louisiana rock salt had been added. Granulation tissue closed the wound within six days; epithelial coverage was completed in about nineteen days.

Observations of sexual behavior totaling ten pre-operative and ten post-operative tests were conducted, each period being ten minutes long. Clark, Aronson & Gordon (1954) found that if proper testing techniques are used, this interval is sufficient to obtain an adequate sample of sexual activity in this species. At the start of each test, a previously isolated virgin female (or a non-virgin that had been isolated for at least eight months) was placed in the male's aquarium. The frequency, time, and sequence of behavior events were recorded on a specially constructed twenty-pen Esterline-Angus graphic recorder (Clark, Aronson & Gordon, 1954). A lapse of eight days was allowed between the operation and the first of the post-operative tests that followed. During this period, all operates were grossly examined and appeared to have regained their health.

The behavioral patterns observed, as described by Clark, Aronson & Gordon (1954) and Schlosberg, Duncan & Daitch (1949), are

summarized below. Each behavior is preceded by an abbreviation, which later accompanies the descriptions of the lesions.

Gonopodial swinging (Sw.)—a forward movement of the male's gonopodium in conjunction with one pelvic fin; performed when the male is not swimming close to the female.

Thrusting (T.) (Tc = contact thrust; Tn = non-contact thrust)—a gonopodial swing directed toward the genital opening of the female. The gonopodium may or may not come in contact with the female's genital opening. During thrusting, spermatophores are not transferred to the female's genital tract.

Copulation (C.)—a prolonged contact thrust often resulting in the transfer of spermatophores to the female.

Pecking (P.)—a rapid series of biting movements at the gravel on the bottom of the aquarium.

Sidling (S.)—the male swims close to the female and tilts his body slightly so that his mid-ventral region is close to the genital area of the female.

Nipping (N.)—the male pursues the female and nips her body especially about the head and genital region; closely associated with aggressive behavior.

Retiring (R.)—usually after swinging or thrusting, a slow or rapid backward swimming away from the female until the male strikes some surface. The male then settles gradually to the bottom of the tank and remains quiescent before resuming activity.

Quivering (Q.)—a rapid up-and-down or side-to-side movement of the male's entire body, which is held in an S-shaped curve, the dorsal and caudal fins folded.

S-curving (Sc.)—an extreme tensing of the fish's body into a simple arc or S-shaped curve.

After each observed copulation, females were examined for sperm by an oviduct smear technique (Clark & Aronson, 1951; Clark, Aronson & Gordon, 1954). Inseminated females were not reused in tests.

Shortly after the last post-operative observation, the brains were removed, fixed in 10% formalin, embedded in paraffin and sectioned transversely at ten μ . Sections were stained with gallocyannin (Einarson, 1932). With a projection microscope, outline drawings were made of approximately every tenth section of each brain. By comparing these drawings with a similarly constructed normal series, the extent of

brain damage was estimated. The description of the operate lesions as well as an analysis of the normal neural configuration of the platyfish forebrain are presented here as an appendix to the paper.

The intact portions of the forebrains exhibited considerable plasticity after operation. This was particularly true after unilateral decerebration, where the remaining lobe was found to occupy a central position and the nuclear patterns were profoundly distorted. For this reason our attempts to estimate, by means of planimeter readings from the serial projections, the mass of forebrain ablated proved unreliable.

RESULTS

The changes in behavior following forebrain deprivation are summarized in Table 1. The average score per test for the ten pre-operative tests for each item of behavior described above and for each fish are compared with the average post-operative scores. It may be noted that all of the sexual patterns except swinging decreased markedly in frequency of occurrence post-operatively. Copulation dropped most of all, appearing in low frequency in only three animals. On the other hand, thrusting behavior, which normally precedes copulation and is always a sign of a sexually aroused animal, dropped only about 33%, and swinging, which is also a sign of sexual excitability, did not decrease at all, even in some of the operates with the most extensive extirpations. Sidling, which usually precedes thrusting, decreased only slightly. Nipping, pecking and quivering, which are often referred to as courtship activities and are primarily synchronizing processes, declined only moderately. In contrast, S-curving and retiring, which are more closely associated with aggressive actions, were reduced most drastically and almost entirely disappeared from the males' repertoire. In five males (nos. 7, 9, 15, 17 and 44) there was a decided post-operative increase in swinging, sidling and thrusting, which are the best indicators of heightened sexual arousal.

There seemed to be a tendency for thrusting behavior to disappear completely or to be greatly reduced in frequency in those fishes in which the deprivation included all or most of the dorsal olfactory areas (nos. 11, 14, 17, 20, 41, 54, 57, 58). However, this distinction was not absolute and there was one outstanding exception, namely, male no. 17 whose forebrain had been completely ablated except for remnants of the preoptic nuclei. This operated male exhibited a high frequency of thrusting and other sexual patterns, and copulated once. Conversely, with the exception of male no. 17, whose thrusting scores increased after operation, an appreciable

portion of the dorsal olfactory area remained intact. In those males with less extensive lesions, where a considerable portion of the dorsal olfactory area was uninjured, thrusting and other sexual activities decreased to a lesser extent. In four of the operated males (nos. 15, 16, 49, 51), one or both olfactory bulbs remained intact. As a group these four males did not differ in their sexual responses from those completely deprived of olfactory sensations.

There was no indication that the presence or absence of the preoptic area had any marked effect on the level and persistence of sexual behavior as suggested by Aronson & Noble (1945) in their work on the grass frog *Rana pipiens*.

During some observations, males nos. 5, 7, 19, 50 and 55 occasionally exhibited a peculiar parallel swimming movement which differed substantially from sidling. Thrusting never followed this aberrant behavior.

DISCUSSION

Although critical experiments concerning sensory processes involved in sexual behavior in poeciliid fishes are not available, it is apparent to anyone working with these species that vision is of prime importance and that olfaction is of lesser importance. This is supported by our finding that several of the operated males exhibited a considerable amount of sexual activity, including copulation, in the complete absence or disruption of the olfactory apparatus.

The idea is still prevalent that the forebrain of fishes is primarily concerned with the organization of olfactory impulses, and for the same reason the prevailing terminology for many forebrain regions, nuclei and tracts includes the term "olfactory." One explanation for this apparent misconception is the over-generalization of the term "fishes." Actually, fishes are phylogenetically very old, and different groups of them have been following divergent evolutionary paths for a very long time. This is expressed in a great number of physiological and morphological differences, among them forebrain structure and function. It is clear that in many families of fishes, the olfactory function of the forebrain has become greatly limited or modified.

Vision is also poorly represented in the forebrain. Definitive fiber tracts from the tectal and diencephalic optic centers to the forebrain have not been demonstrated. Yet surgical invasion of the forebrain materially reduces what are thought to be essentially visually directed processes. On the other hand, the entire pattern of sexual behavior was elicited in a few instances

TABLE 1. AVERAGE FREQUENCY OF SEXUAL PATTERNS BEFORE AND AFTER FOREBRAIN OPERATIONS^a

Male No.	Gonopodial Swinging		Thrusting		Copulation		Pecking		Sidling		Nipping		Quivering		S-curling		Retiring		
	Pre.	Post.	Pre.	Post.	Pre.	Post.	Pre.	Post.	Pre.	Post.	Pre.	Post.	Pre.	Post.	Pre.	Post.	Pre.	Post.	
3	7.7	12.5	4.7	2.6	0.0	0.0	4.4	3.2	3.4	2.6	5.9	0.1	0.5	0.0	0.2	0.0	0.3	0.1	
5	11.6	10.7	70.4	37.1	0.6	0.0	14.8	6.1	17.5	19.2	2.4	0.1	0.6	0.1	0.1	0.0	0.9	0.1	
7	2.5	10.5	18.3	22.1	0.3	0.0	0.9	5.0	6.6	13.2	0.3	0.1	0.2	0.3	0.2	0.0	0.3	0.0	
9	2.5	8.6	0.0	16.4	0.0	0.0	0.1	0.7	0.2	7.8	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
11	5.9	0.0	19.4	0.0	0.3	0.0	0.7	0.0	2.6	0.0	0.0	0.0	0.4	0.0	0.1	0.0	0.2	0.0	
12	7.5	3.6	16.3	0.1	0.6	0.0	2.3	1.8	6.9	4.3	0.3	0.1	0.1	0.2	0.6	0.0	0.8	0.0	
13	15.6	11.2	5.5	21.0	0.2	0.0	8.7	1.2	4.5	10.2	0.0	0.1	0.2	0.0	0.4	0.0	0.2	0.0	
14	13.5	0.8	11.4	0.0	0.1	0.0	4.0	0.3	2.8	0.0	0.9	0.0	0.0	0.0	0.2	0.0	0.0	0.0	
15	9.5	11.6	16.9	19.6	0.2	0.0	3.1	2.6	6.0	8.7	1.3	0.1	0.0	0.1	1.4	0.1	0.0	0.8	
16	9.4	8.7	5.3	3.7	0.4	0.0	2.3	1.3	5.0	2.6	1.4	0.1	0.4	0.0	1.0	0.0	0.3	0.1	
17	4.6	8.1	16.7	95.9	0.9	0.1 ^b	2.4	13.9	8.7	34.2	0.6	0.3	0.5	0.2	0.5	0.0	0.3	0.0	
18	5.8	5.3	14.2	11.5	0.2	0.0	2.1	0.8	9.9	7.1	0.4	0.3	0.0	0.1	0.4	0.0	0.0	0.1	
19	6.7	8.8	31.3	18.4	0.2	0.0	1.9	0.0	11.4	9.2	0.6	0.3	0.5	0.2	1.6	0.0	0.1	0.0	
20	14.8	1.2	40.6	0.0	0.3	0.0	5.5	0.1	14.8	0.1	1.2	0.0	0.0	0.0	0.1	0.1	0.2	0.0	
41	6.0	7.4	22.7	5.4	0.5	0.0	8.4	0.1	8.9	3.8	3.1	0.0	0.2	0.0	0.2	0.0	0.4	0.0	
44	3.2	10.4	13.1	15.2	1.1	0.2 ^c	3.6	4.4	4.5	3.8	0.6	1.1	1.0	0.2	0.1	0.1	0.3	0.2	
45	9.5	7.8	40.2	20.6	1.2	0.0	5.4	0.7	19.6	5.1	0.0	0.2	0.7	0.0	0.4	0.1	0.8	0.0	
49	6.2	7.2	9.5	2.4	0.0	0.1 ^c	0.3	1.1	6.5	3.2	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	
50	4.2	5.9	33.8	0.0	0.0	0.0	0.2	0.5	11.4	3.7	0.0	0.0	1.5	0.0	0.4	0.0	1.1	0.0	
51	5.6	10.0	135.0	7.0	1.5	0.0	2.1	4.7	16.7	12.9	2.6	6.1	1.3	0.8	1.1	0.1	1.0	0.0	
53	19.7	12.0	131.6	23.5	1.1	0.0	0.5	0.0	41.3	13.5	0.5	0.0	0.7	0.0	0.3	0.0	0.6	0.0	
54	5.7	10.5	32.7	0.0	2.1	0.0	0.1	0.4	13.9	0.1	0.4	0.0	0.6	0.0	0.5	0.0	1.1	0.0	
55	8.2	7.4	38.4	1.9	3.1	0.0	3.0	0.2	15.8	1.5	0.1	0.2	1.5	0.0	0.6	0.1	2.3	0.0	
57	12.8	19.6	23.9	0.0	0.8	0.0	1.7	0.1	10.6	0.6	0.4	0.1	0.6	0.0	0.4	0.0	0.8	0.0	
58	7.0	11.5	49.1	3.7	1.1	0.0	0.0	0.4	16.5	3.8	0.2	0.1	0.0	0.0	0.5	0.0	0.9	0.0	
59	11.9	10.0	25.4	0.5	0.7	0.0	0.0	0.4	10.6	1.3	0.8	2.6	0.6	0.0	0.6	0.0	0.9	0.1	
61	9.7	13.9	10.3	0.0	0.0	0.0	0.0	0.3	5.1	0.3	0.6	0.0	0.0	0.0	0.1	0.0	0.1	0.1	
Means	8.4	8.7	32.1	11.2	0.7	0.01	3.0	1.8	10.5	6.3	1.0	0.5	0.4	0.1	0.4	0.03	0.5	0.04	
MEAN																			
DIFF $\pm\sigma$	0.3 \pm 1.1 ^d		20.9 \pm 7.2 ^e		0.7 \pm 0.2 ^f		1.2 \pm 0.9 ^d		4.2 \pm 1.8 ^e		0.5 \pm 0.8 ^e		0.3 \pm 0.1 ^f		0.4 \pm 0.08 ^f		0.5 \pm 0.1 ^f		0.5 \pm 0.1 ^f

^a Based on 10 pre-operative and 10 post-operative observations, each 10 minutes long, for each male except male 19 which had only 9 pre-operative tests.

^b Female not inseminated.
^c Female inseminated.
^d $P > .05$
^e $P > .01 < .05$
^f $P < .01$

in animals with total (or almost complete) absence of the forebrain.

These thoughts lead to the hypothesis that the forebrain does not function directly in the organization of sexual behavior patterns, but rather that it acts as a generalized sensitizer, or facilitator of centers and mechanisms lower in the brain. This is undoubtedly what certain of the earlier authors, mentioned in the introduction, described as loss of "initiative," etc. A facilitative action of the forebrain was also proposed in a study of brain function in relation to spawning in the mouthbreeding fish *Tilapia* (Aronson, 1948) and in the grass frog *Rana pipiens* (Aronson & Noble, 1945). Beach (1951) reached a similar conclusion following a study of brain injury and mating in male pigeons, and Beach (1942) and Lashley (1930) have extensive evidence for this type of action of the cerebral cortex of mammals. Herrick (1948), in a discussion of the evolution of the cerebral cortex, expressed the belief that this sensitizing action of the forebrain develops from parts of the original olfactory areas which lack localizing functions and to which ascending and descending pallial projection fibers were added during phylogenetic development. Thus it is evident that at least one fundamental component of mammalian cortical activity must have made its appearance very early in vertebrate history.

In an earlier study, Clark, Aronson & Gordon (1954) demonstrated that gonopodial swinging in male platyfish is directly correlated with thrusting and copulatory behavior. Males having low scores for swinging rarely thrust or copulated, and conversely those males with high scores for thrusting and copulation also exhibited a considerable amount of swinging. This behavior may therefore be used as an indicator of the degree of sexual arousal. These observations have a direct bearing on our finding in the present experiment that swinging scores were not adversely affected by forebrain deprivations. Thus we may conclude that for the most part the operated males were aroused to a degree equal to or better than before the operations, and the possibility that the proximity of the lesions to the pituitary gland may have adversely affected pituitary and gonadal function is thereby minimized.

Clark, Aronson & Gordon also found that gonopodial swinging is the only component of sexual behavior in platyfish which appears in completely isolated males. All the other sexual patterns are directly oriented toward the female (or another male). This is most likely a visual orientation, and it suggests once more that in these fishes the forebrain deprivations might be affecting primarily the visual processes associ-

ated with sexual behavior. The experiments of Aronson & Noble (1945) form an interesting parallel. In laboratory aquaria, male frogs implanted with one or more pituitary glands readily swim to, clasp and spawn with ovulated females. The first component, namely swimming to the female, is based on visual orientation. The remaining components are mediated by contact stimulation. Completely decerebrated frogs activated by pituitary implantation will not swim to the ovulated female even if she is close by. If the male should accidentally touch the female as he swims about the tank, however, he will rapidly turn and clasp the female, and then the rest of the spawning will proceed normally. Here, too, forebrain deprivation has its effect on the visual component of the sexual process. Finally we may recall the observation of Wiebalck (1937) who found that schooling, which is a visually directed response, was impeded in forebrainless fish.

SUMMARY AND CONCLUSIONS

Each of 27 mature male platyfish was paired with a mature female for ten tests, each of ten minutes duration. Quantitative records of various patterns of sexual behavior were made. Lesions of various dimensions were then made in the forebrains of all the males, after which the fish were given ten equivalent post-operative tests.

In general, all of the sexual acts except gonopodial swinging declined in frequency after operation, but a few males maintained a considerable level of sexual activity, even after extensive forebrain deprivation. There was no indication that any of the sexual patterns could be completely eliminated by forebrain removal.

It is concluded that the forebrain facilitates the activities of lower parts of the brain, particularly in relation to visually directed responses.

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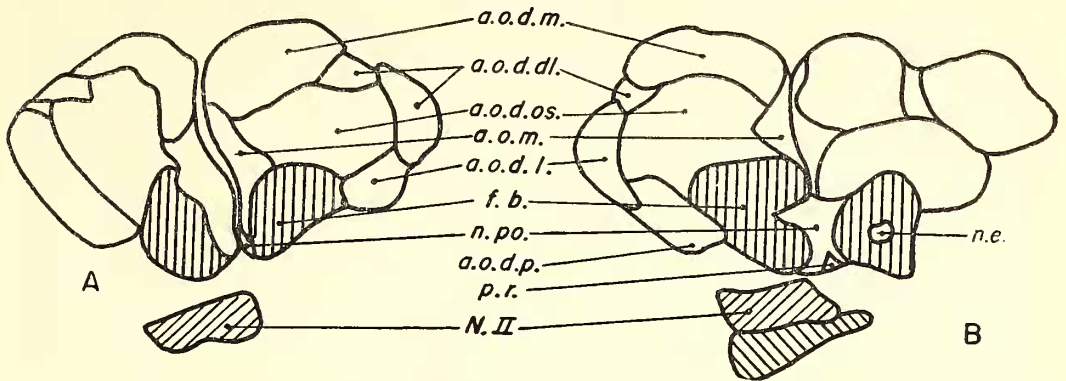
APPENDIX

A description of the forebrain of the platyfish is not available, nor has this region been studied in any related cyprinodont species. Therefore, in delimiting the extent of the lesions, the description by Kappers, Huber & Crosby (1936) of the nuclear configuration of the telencephalon of the sunfish was used. A few notable differences were observed:

1. The pars dorsolateralis of the dorsal olfactory area is much more extensive than in the sunfish and is subdivided into several discrete nuclei. Meader (1939) and Aronson (unpublished) have noted similar or more extensive enlargements and differentiations in a number of highly specialized teleosts.

2. The medial olfactory area is divided into several pre- and post-commissural nuclei.

3. The cells in the posterior lateral portion of the forebrain are distinctly separated from the pars lateralis of the dorsal olfactory area



TEXT-FIG. 1. Outlines of cross-sections through the forebrain of *Xiphophorus maculatus*, (A) anterior to the anterior commissure, and (B) posterior to the anterior commissure.

Abbreviations

a.o.d.dl. —area olfactoria dorsalis, pars dorsolateralis
 a.o.d.l. —area olfactoria dorsalis, pars lateralis
 a.o.d.m. —area olfactoria dorsalis, pars medialis
 a.o.d.os. —area olfactoria dorsalis, pars olfactosomatica

a.o.d.p. —area olfactoria dorsalis, pars posterior
 a.o.m. —area olfactorius medialis
 f.b. —medial and lateral forebrain bundles
 N. II —optic nerve
 n.e. —nucleus entopeduncularis
 n.po. —nucleus preopticus
 p.r. —preoptic recess

and are referred to here as the *pars posterior of the dorsal olfactory area*. This nucleus is probably homologous to the lobus pyriformis of Sheldon (1912) and has been variously named by other authors.

4. The *pars magnocellularis* of the nucleus preopticus cannot readily be distinguished from the parvocellular portion. This is atypical for teleosts.

The major nuclei of the platyfish forebrain that are referred to in the following descriptions of the lesions are shown in Text-figure 1. In the following descriptions of the lesions, the olfactory bulbs were either ablated, damaged beyond clear recognition, or were completely separated from the forebrain, except where specifically noted.

Male 3. (Sw, Tc, P, S, N, R)³. Dorsal olfactory areas ablated except for (1) *pars posterior* on right side, (2) a portion of *pars posterior* on left side and (3) portions of *pars olfacto-somatica*. Medial olfactory areas intact; preoptic nuclei intact.

Male 5. (Sw, Tn, P, S, N, Q, R). Dorsal olfactory areas ablated except for remnants of *pars posterior* and *pars olfacto-somatica*. Medial olfactory areas and preoptic nuclei intact. Slight invasion of anterior surface of right tectum.

Male 7. (Sw, Tn, P, S, N, Q). Dorsal olfactory areas ablated except for (1) remnant of *pars posterior* on right side and (2) small portions of *pars lateralis*, *pars posterior* and *pars olfacto-somatica*.

³ These abbreviations refer to the behavior patterns exhibited by each male in the post-operative tests.

Medial olfactory area invaded on right side; preoptic nuclei intact.

Male 9. (Sw, T, P, S). Left lobe of forebrain ablated except small part of medial olfactory areas. On right side dorsal olfactory area ablated except for (1) remnant of *pars lateralis* and (2) most of *pars posterior*. Right medial olfactory areas intact; preoptic nuclei intact.

Male 11. Forebrain completely ablated except for remnant of *pars posterior* of dorsal olfactory area and preoptic nuclei.

Male 12. (Sw, Tn-Tc, P, S, N, Q). Dorsal olfactory areas ablated except for small portions of *pars olfacto-somatica* and *pars posterior*. Medial olfactory areas almost intact; preoptic nuclei intact.

Male 13. (Sw, Tn, P, S). In right lobe, dorsal olfactory area extensively invaded at posterior pole, but *pars medialis*, *pars lateralis* and *pars olfacto-somatica* largely intact at the anterior end; in left lobe only remnants of dorsal olfactory area were found; medial olfactory area invaded dorsally on right lobe and completely destroyed on left lobe; preoptic nuclei intact.

Male 14. (Sw, P). Forebrain ablated except for small remnants of medial olfactory areas and *pars posterior* of dorsal olfactory areas; preoptic nuclei intact.

Male 15. (Sw, Tn-Tc, P, S, N, Q, R). On right side dorsal olfactory area destroyed except for remnants of *pars olfacto-somatica*. On left side dorsal olfactory area intact except for slight dorsal invasion; olfactory bulb intact. Dorsal portion of medial olfactory area invaded; preoptic nuclei intact.

Male 16. (Sw, Tn-Tc, P, S, N, R). Dorsal olfactory areas of both lobes mostly ablated; medial

olfactory areas almost completely intact; olfactory bulb on right side intact; preoptic nuclei intact.

Male 17. (Sw, Tn-Tc, C, P, S, N, Q). Forebrain entirely ablated except for small remnants of preoptic nuclei.

Male 18. (Sw, Tn, P, S, N, Q, R). On right side pars medialis of dorsal olfactory area ablated. Rest of dorsal olfactory area intact except for some invasion at the anterior pole; on left side dorsal olfactory area mostly ablated. Medial olfactory area of both lobes largely intact; preoptic nuclei intact.

Male 19. (Sw, Tn, S, N, Q). Dorsal olfactory areas destroyed except for the pars posterior and remnant of pars medialis. Medial olfactory areas ablated except for small remnants; preoptic nuclei intact.

Male 20. (Sw, P, S). Forebrain completely ablated except for (1) a small remnant of medial olfactory areas and (2) the preoptic nuclei.

Male 41. (Sw, Tn, P, S). Forebrain ablated except for (1) a small dorsal portion of the medial olfactory areas and (2) the preoptic nuclei.

Male 44. (Sw, Tn, C, P, S, N, Q, R, Sc). Dorsal olfactory areas ablated except for the pars olfacto-somatica and a portion of the pars posterior of the right lobe. Medial olfactory areas and the preoptic nuclei intact.

Male 45. (Sw, Tn, P, S, N, Sc). Forebrain completely ablated except for (1) remnants of the pars posterior of the dorsal olfactory areas, (2) portions of the medial olfactory areas and (3) the preoptic nuclei.

Male 49. (Sw, Tn, C, P, S, N, Q). Right lobe ablated except for (1) a portion of medial olfactory areas and (2) the preoptic nuclei. Left lobe intact except for slight invasion of pars lateralis of dorsal olfactory area. Left olfactory bulb intact.

Male 50. (Sw, P, S). Forebrain ablated except for (1) parts of the medial olfactory areas, (2) remnants of the pars olfacto-somatica and pars

posterior of the right dorsal olfactory area and (3) the preoptic nuclei.

Male 51. (Sw, Tn, P, S, N, Q, Sc). Left lobe ablated except for (1) a remnant of pars lateralis of dorsal olfactory area, (2) most of medial olfactory area and (3) the preoptic nuclei. Right lobe intact except for slight lesion of pars medialis of dorsal olfactory area. Right olfactory bulb intact.

Male 53. (Sw, Tn, S, Sc). Dorsal olfactory areas ablated except for the pars olfacto-somatica, the pars posterior and a portion of the pars lateralis of the dorsal olfactory area of the right side. Most of the medial olfactory areas and the preoptic nuclei intact.

Male 54. (Sw, P, S). Forebrain completely ablated except for caudal remnant of the preoptic nuclei; habenular nuclei and anterior dorsal edge of diencephalon destroyed; slight lesion in anterior pole of left tectum.

Male 55. (Sw, Tc, P, S, N, Sc). On right side dorsal olfactory area ablated except for remnant of pars posterior. On left side portions of the pars medialis, pars lateralis, pars posterior and pars olfacto-somatica remain. Medial olfactory areas mostly intact; preoptic nuclei intact.

Male 57. (Sw, P, S, N). Forebrain completely ablated except for caudal ends of preoptic nuclei.

Male 58. (Sw, Tn, P, S, N). Same as 57.

Male 59. (Sw, Tc, P, S, N, R). On right side dorsal olfactory area ablated except for olfacto-somatica area and pars posterior which are largely intact. On left side dorsal olfactory area completely missing. Medial olfactory areas mostly intact; preoptic nuclei intact.

Male 61. (Sw, P, S, R). On right side dorsal olfactory area ablated except for remnants of pars lateralis, pars posterior and pars olfacto-somatica. On left side dorsal olfactory area ablated except for remnant of pars posterior. Medial olfactory areas mostly intact; preoptic nuclei intact.